THE EMBRYOLOGY OF THE APTERYGOTA.

AGNES M. CLAYPOLE, PH.D.

UP to within the last few years comparatively little work has been done on the embryology of the lowly insect forms included in Brauer's group Apterygota, and until we reach the recent date of 1892 no studies of serial sections have been reported. Hence there are among earlier works many misinterpretations of superficial features. Much of the early work was done on members of the subdivision Collembola, including the more lowly apterygote insects. The first contribution came from the systematist Nicolet. Unfortunately, but meager data of this article have been obtained. It can merely be stated that some time previous to 1869 Nicolet published studies on *Podura aquatica*, *Desoria cinerea*, *Cyphodeirus agilis*, *Sminthurus ornatus*, and *Orchesella* sp(?). He established three facts: that holoblastic cleavage exists among the Collembola; that their eggs are spherical; that an amnion and serosa are wanting.

In 1871 Packard[1] gave the results of studies on the form *Isotoma walkeri*, not a thysanuran, but a collembolan. Only the stages after germ-band formation are mentioned. This is said to arise as a complete girdle and to show early 6–7 segments. These were identified as antennae 1, mandibles 1, maxillae 1, with possibly a second, thoracic legs 3. Later rudiments of a spring appear on the fifth abdominal segment; an unpaired median labrum is also developed. At no time are any tracheae present, and the larvae on leaving the egg resemble the lower Collembola more than the adult Isotoma. A cuticle like that of crustaceans appears during development.

In 1875 Oulganine[2] published studies on *Achorutes tuberculatus* Nic., *Anurophorus fimetarius*, and two species of Degeeria.

[1] Packard, Jr., A. S., "Embryological Studies on Diplax, Perithemis, and the Thysanurous Genus Isotoma," *Peabody Acad. Sci.* No. 11. 1871.

[2] Oulganine, W., "Sur le Développement des Podurelles" (Extrait du Russe par M. de Korotneff), *Arch. de Zool. Exper.* Tome iv. 1875.

The eggs all undergo equal holoblastic cleavage, resulting in a uniform single-layered blastoderm soon rendered many layered by rapid growth. The surface becomes crenated and ridged and forms a cuticle, also crenated. The blastoderm becomes smooth, and outlines of the embryo appear. The second embryonic layer is said to arise from a definitely placed area lying between the head and tail of the belt-like germ band. A "dorsal organ" is probably present, though not described as such. Nine pairs of appendages appear: antennae 1, mandibles 1, maxillae 2, thoracic legs 3, abdominal 2. One pair of those on the abdomen forms the collophore, and the other the spring. Poduridae are found to resemble the lower arthropods in the following respects: (1) holoblastic cleavage; (2) absence of amnion; (3) possession of blastodermic cuticles; (4) the formation of the intestine from the middle germ layer.

In 1882 Lemoine[3] added studies on the Collembola *Anurophorus laricis* and *Sminthurus plumbeus*, two species differing widely from each other in habits and form. The first is small, springless, inactive, and colonial, while the second is large, with a well-developed spring, active, and solitary. The eggs of Anurophorus found in April and May were clear and easy to observe, while those of Sminthurus found in November and December were slow in development and difficult to study. Superficial cleavage, accompanied by secondary yolk cleavage, was true of the former, and the latter showed very unequal holoblastic cleavage with a blastoderm early formed of two layers. "Dorsal organs" appear in both, persisting up to the time of hatching. The entoderm is said to arise from two inpittings, one in front and one behind the "dorsal organ" and at several other places on the periphery. The germ band, at first forming a belt surrounding the whole circumference of the egg, shows 12–13 segments: 1 cephalic, 3 mandibular, 3 thoracic, and 5–6 abdominal. Two membranes appear, one of which is clearly connected with the "dorsal organ." A collophore develops in both forms, but the spring is rudimentary in Anurophorus, a condition also true of the tracheal system.

[3] Lemoine, P., "Recherches sur le Développement des Podurelles," *Ass. Franc. p. advanc. des Sci.* La Rochelle. 1882.

Grassi[4] gives the first mention of thysanuran development. He describes three features in the developmental processes of Japyx. The cleavage is distinctly superficial; an amnion exists, and also a "dorsal organ."

Ryder[5] published studies on *Anurida maritima* Guen., giving the following results. After the formation of the germ band two membranes invest the embryo, the inner one being crenated. The embryonic area forms a nearly complete belt surrounding the egg, and seven pairs of appendages can be made out: antennae 1, mandibles 1, maxillae 1, thoracic legs 3, and the collophore on the first abdominal segment. A rudimentary spring is reported as still visible on the fourth abdominal segment of the hatched larva, but no trace remains in the adult.

Wheeler[6] gives the first account of section views of an apterygote insect. He shows the existence of an intercalary segment with appendages in the head of *Anurida maritima*, placed between the mandibular and antennal segments. The "dorsal organ" is shown in section and is definitely homologized with the "indusium" of Xiphidium.

Later studies all include internal structure as seen in sections. In 1896 Heymons[7] published a short account of his work on *Lepisma saccharina*, the highest of the Thysanura. The eggs of this species are oval and about 1 mm. in their longest diameter; cleavage is distinctly superficial, and an extremely small germ band early appears. This is found to sink immediately into the yolk, still, however, retaining its connection with the serosa, the extraembryonic part of the blastoderm, by a thin membrane, the amnion. As the embryo sinks in, the amniotic cavity becomes large and distinct, but always retains connection with the outside by the open amnion pore. The amnion is hence never constricted from the serosa. By later growth of the germ band the pore is opened and the amnion is retracted

[4] Grassi, B., "I Progenitori degli Insetti e dei Miriapodi l'Japyx e la Campodea," *Atti accad. Givenia Sci. Nat. in Catania.* (3), vol. xix. 1885.

[5] Ryder, J. A., "The Embryology of Anurida Maritima Guen.," *Amer. Nat.* Vol. xx. 1888.

[6] Wheeler, W. M., "A Contribution to Insect Embryology," *Journ. of Morph.* Vol. viii, No. 1. 1893.

[7] Heymons, R., "Ein Beitrag zur Entwicklungsgeschichte der Insekten Apterygota," *Sitz. Berichte Acad. Wiss.* Berlin. 1896.

to form a "dorsal organ" similar to the structure of that name in the pterygote insect. The author proves two points: (1) that Thysanuran cleavage is superficial, differing from the Collembolan type, and (2) that embryonic membranes are formed homologous with those of the Pterygota. Hence Lepisma is an intermediate form transitional between the Collembola and higher insects.

This paper is followed in 1897 by a longer and more complete study of the same form at the hands of the same worker, Heymons.[8] In this he shows that some of the cleavage nuclei migrate from the center to form the blastoderm, while others remain in the yolk as yolk-cells. The gastrula has the form of a circular depression instead of the typical groove, and as soon as a two-layered condition is attained the germ band sinks into the yolk. While buried in the yolk the germ-band segments and paired appendages appear. First antennae, post-oral in position, next distinct intercalary appendages, mandibles, and two pairs of maxillae with a median unpaired labrum. The maxillae early split in two longitudinally, and the maxillary palps remain clearly homologous with the thoracic legs. Paired abdominal appendages appear on each segment except the 11th, getting progressively smaller from the first pair to the 10th. After several weeks the larvae hatch and are chiefly distinguished from the adults by their white color and the absence of the styli and cerci.

The reproductive cells appear at an early stage in the hind end of the embryo and are clearly of ectodermic origin; after much migrating they enter the primitive somites and form follicles segmentally arranged in the female. The mesenteron was described as arising from yolk-cells that migrate from the yolk and multiply to form a continuous layer enclosing the yolk and is hence entodermal in origin. In conclusion it is clear that the Thysanura show strongly marked pterygote peculiarities, and the conditions described suggest the author's opinion that the formation of embryonic envelopes is due to increase of yolk material in the egg.

[8] Heymons, R., "Entwicklungsgeschichtliche Untersuchungen an Lepisma saccharina L.," *Zeitschr. f. wiss. Zool.* Bd. lxii. 1897.

At almost the same time Uzel[9] published a series of articles on the two forms Campodea and Lepisma. His work on the latter practically confirms that of Heymons and may be omitted from this review. He determines that the eggs of Campodea are spherical, about 0.4 mm. in diameter, undergo superficial cleavage, resulting in a blastoderm spread uniformly over the whole surface. No secondary yolk cleavage exists. The germ band arises by migration of cells from all parts of the blastoderm to form a belt encircling nearly the whole egg. A "dorsal organ" appears between the head and the tail, but neither an amnion nor a serosa is developed. Paired appendages are early distinguished, also a median unpaired labrum. Of the paired appendages the following are found: one pair of antennae, a pair of distinct intercalary appendages, one pair of mandibles, two pairs of maxillae, three pairs of thoracic feet, and nine pairs of abdominal structures. An interesting point is noted in the permanent retention of the intercalary appendages as lateral folds round the adult mouth. Later the 1–7th abdominal appendages split longitudinally, the outer part forming the permanent styli and the inner the abdominal sacs.

There is to appear in the new *Journal of Morphology*[10] a paper giving the results of my studies on *Anurida maritima.* Merely a summary of the most important points will be included in this consideration. It was found that the ovary was extremely simple in form, like that of a myriapod. Each ovum is associated with nutritive cells and the germinal vesicle early disappears. The egg is spherical, about .27 mm. in diameter, with at first slightly unequal holoblastic cleavage; this is eventually lost after a large-celled morula stage has been formed, and the blastoderm rises by migration, as in eggs with superficial cleavage. It assumes a two-layered condition at once, the entoderm remaining dormant in the yolk. A "dorsal organ" is formed between the two ends of the belt-like germ band, the latter early showing the usual pairs of appendages

[9] Uzel, H., "Vorläufige Mittheilungen über die Entwicklung der Thysanura. Beiträge zur Entwicklungsgeschichte von Campodea staphilinus," *Zool. Anz.* Nrs. 125, 128, 135. 1877.

[10] Claypole, A. M., "The Oögenesis and Embryology of Anurida Maritima," *Journ. of Morph.* Vol. xiv. 1898.

together with a pair on the intercalary segment which takes part in the formation of the adult mouth. These are homologized with the second pair of Crustacean antennae. Yolk is found enclosed with reproductive cells, causing their very rapid development. Anurida agrees with the rest of the Collembola in showing characters allying it strongly with the lower arthropods.

Summing up the present state of knowledge regarding Apterygote embryology, it is found that at least fourteen species of Collembola and three of Thysanura have been studied with more or less care. This work confirms by its results the opinion that the Apterygota possess truly primitive characters and also show transitions to the higher and lower Arthropoda. Cleavage among the Collembola, as far as determined, shows many types: equal holoblastic, unequal holoblastic, holoblastic becoming superficial, and truly superficial; while on the other hand the Thysanura show only the superficial type, whether the eggs are spherical or oval. It is unfortunate that in most cases the size of the eggs is not given, and in many instances the method of cleavage is unknown. Still a comparison of the three available forms is instructive.

ANURIDA. Spherical, .27 mm. in diameter. Cleavage holoblastic becoming superficial.

CAMPODEA. Spherical, .4 mm. Superficial cleavage.

LEPISMA. Oval, 1. mm. Superficial cleavage.

The apparent discrepancy between the two sizes given for the eggs of Anurida by Ryder and myself is readily explained by the fact that the measurements were taken at different stages. There is a marked increase in size during development. No early stages are described for Isotoma, whose size is the smallest yet recorded (.15 mm.), but some of Packard's so-called germ-band figures suggest strongly that they are possibly stages showing the first cleavage plane appearing. Enough is given in this short series to indicate a regular increase in the size of the egg and a *pari passu* loss of holoblastic cleavage in passing up the scale of apterygote insects. The only trace of the total cleavage remaining in Lepisma is shown in the yolk

cleavage; it is markedly significant that nothing of this kind occurs in Anurida after the holoblastic condition is lost, though the yolk is fused into a solid mass and nuclei are scattered through it; such secondary cleavage is reported in Anurophorus, where egg cleavage is superficial.

It is equally clear that the amnion and serosa are absent in the Collembola, the embryonic membranes formed having the nature of "Blastodermhäuten." In Anurophorus, Achorutes, Degeeria, Sminthurus, and Anurida these membranes show some amount of crenation and hence have powers of expansion. In all cases they are found in connection with the so-called "dorsal organ," which is a structure clearly homologous throughout the Collembola, being similarly placed and similar in development. A similar structure, similarly placed, is also found in Campodea and Japyx. Heymons considers the "dorsal organ," caused by the invaginating cellula envelopes, homologous with these. But the distinct and early appearance of this organ and the simultaneous presence of the amnion and serosa in Japyx and Campodea are clear evidences against such an homology. This is still further confirmed by reference to the structure described by Wheeler as the "indusium"; this is without doubt, as he states, the homologue of the apterygote "dorsal organ," and is certainly distinct from the structure that rises later during the elimination of embryonic envelopes. It is possible that a structure similar to the earlier stages of the indusium may exist in Lepisma, but no such specialized later developments would be expected as those found in the Orthoptera.

It is also interesting to see the clearness with which certain facts are indicated as to the appearance and fate of certain appendages. The collophore is without doubt a fused pair of abdominal feet; the spring has a similar origin on the fourth or fifth abdominal segment, and according to Uzel the styli and ventral bladders rise directly from abdominal appendages. There is almost unanimous evidence that an intercalary segment exists in the apterygote head placed between the antennae and the mandibles, disappearing in some cases but remaining to form permanent mouth-parts in others. It is reasonable to

consider them the homologues of the second pair of Crustacean antennae.

In every way the apterygote insect appears to be truly primitive; no evidences of wings appear, and many points in shape of eggs, cleavage, embryonic membranes, and appendages show resemblances to the lower Arthropoda. One question has been purposely left untouched in this brief review: that of gastrulation. It is only from studies based on sections that safe conclusions can be drawn, and the difficulties introduced by the method of germ-layer formation described for Anurida render further facts necessary concerning these processes in other forms before general principles can be safely deduced.

WELLESLEY COLLEGE,
WELLESLEY, MASS.